

Landscape models to understand steelhead (*Oncorhynchus mykiss*) distribution and help prioritize barrier removals in the Willamette basin, Oregon, USA

E. Ashley Steel, Blake E. Feist, David W. Jensen, George R. Pess, Mindi B. Sheer, Jody B. Brauner, and Robert E. Bilby

Abstract: We use linear mixed models to predict winter steelhead (*Oncorhynchus mykiss*) redd density from geology, land use, and climate variables in the Willamette River basin, Oregon. Landscape variables included in the set of best models were alluvium, hillslope < 6%, landslide-derived geology, young (<40 years) forest, shrub vegetation, agricultural land use, and mafic volcanic geology. Our approach enables us to model the temporal correlation between annual redd counts at the same site while extracting patterns of relative redd density across sites that are consistent even among years with varying strengths of steelhead returns. We use our model to predict redd density (redds per kilometre) upstream of 111 probable migration barriers as well as the 95% confidence interval around the redd density prediction and the total number of potential redds behind each barrier. Using a metric that incorporates uncertainty, we identified high-priority barriers that might have been overlooked using only stream length or mean predicted fish benefit and we clearly differentiated between otherwise similar barriers. We show that landscape features can be used to describe and predict the distribution of winter steelhead redds and that these models can be used immediately to improve decision-making for anadromous salmonids.

Résumé : Des modèles linéaires mixtes utilisant des variables reliées à la géologie, à l'utilisation des terres et au climat nous ont servi à prédire la densité des nids de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) d'hiver dans la rivière Willamette, en Oregon. Les variables du paysage incluses dans la série des meilleurs modèles comprennent l'alluvion, les versants < 6 %, la géologie reliée aux glissements de terrains, les forêts jeunes (<40 ans), la végétation arbustive, les terres agricoles et la géologie volcanique mafique. Notre méthode nous permet de modéliser la corrélation temporelle entre les inventaires annuels de nids à un même site, tout en extrayant des patterns de densité relative des nids à travers les sites qui sont cohérents même entre les années qui ont des retours de truites arc-en-ciel anadromes d'importance inégale. Notre modèle a servi à prédire la densité des nids (nids par kilomètre) en amont de 111 barrières probables à la migration, de calculer l'intervalle de confiance de 95 % autour de la prédiction de densité des nids et d'estimer le nombre total de nids potentiels derrière chaque barrière. À l'aide d'une métrique qui inclut l'incertitude, nous avons identifié des barrières de forte priorité qui ont pu passer inaperçues d'après la seule longueur du cours d'eau ou d'après le bénéfice moyen prédit pour les poissons; cela nous a permis ainsi de différencier clairement des barrières semblables par ailleurs. Nous démontrons que des caractéristiques du paysage permettent de décrire et de prédire la répartition des nids des truites arc-en-ciel d'hiver et que ces modèles peuvent servir dès à présent pour améliorer les prises de décision concernant les salmonidés anadromes.

[Traduit par la Rédaction]

Introduction

Recent advances in modeling the distribution of fish from landform and land use have taken a broad-scale approach (Thompson and Lee 2000; Pess et al. 2002; Feist et al. 2003) that differs from previous site-specific research (e.g., Bus-

tard and Narver 1975; Geist et al. 2000). Site-specific variables such as substrate size or riparian cover clearly are important influences on salmon distribution and abundance. However, factors such as geology and land use can determine the distribution of these site-specific variables and so may have a controlling influence on the distribution of spe-

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E.A. Steel,¹ B.E. Feist, D.W. Jensen, G.R. Pess, M.B. Sheer, and R.E. Bilby.² Northwest Fisheries Science Center, NOAA Fisheries, 2725 Montlake Blvd. East, Seattle, WA 98112, USA.

J.B. Brauner. School of Aquatic and Fishery Sciences, P.O. Box 355020, University of Washington, Seattle, WA 98195, USA.

¹Corresponding author (e-mail: Ashley.Steel@noaa.gov).

²Present address: Weyerhaeuser Company, Tacoma, WA 98477, USA.

cies (Richards et al. 1996). Examining patterns of fish abundance or survival at larger scales can provide new scientific insight regarding factors determining fish distribution (Poff 1997; Poff and Hury 1998). Because data on landscape features are often available more easily than reach-scale data describing in-stream conditions, results of these large-scale analyses may be faster to achieve and can be immediately useful in efforts to manage fish populations (Lunetta et al. 1997).

Landscape-scale analyses have yielded insights into a wide range of aquatic community and fish population metrics including aquatic community composition, salmonid spawner abundances, and juvenile salmonid distribution. Identification of patterns at these scales has been possible across dissimilar ecoregions. Catchment area and low-flow yield were used to explain fish community composition of primarily resident fishes in Michigan State (Zorn et al. 2002). Coho salmon (*Oncorhynchus kisutch*) spawner distribution in the Snohomish River basin, Washington State, can be explained as a function of wetland occurrence, local geology, stream gradient, and land use. As well, juvenile chinook salmon (*Oncorhynchus tshawytscha*) distribution in multiple drainages in Idaho State could be explained as a function of road density and precipitation while juvenile steelhead (*Oncorhynchus mykiss*) abundances in the same basins were correlated with geology (Thompson and Lee 2000). Correlations between juvenile steelhead and geology have also been identified in Oregon Coast Range streams (Hicks and Hall 2003). Landscape-scale studies have enabled comparisons between past and present land use. An analysis of patterns over whole watersheds identified links between past land-use patterns and present-day fish and invertebrate diversity in western North Carolina State (Harding et al. 1998).

We use linear mixed models to examine relationships between landscape characteristics such as geology, land use, and climate and the distribution of winter steelhead redds in four watersheds that comprise 23% of the Willamette River basin, Oregon. Steelhead exhibit a varied life history pattern that has made habitat generalizations difficult. Our statistical technique allows us to model the temporal correlation between annual fish observations at the same site while extracting patterns of relative redd density across sites that are consistent among years with varying strengths of steelhead returns. Using this technique, we are able to develop correlative models that describe landscape traits associated with areas of high steelhead spawner abundance and that can predict where in the study watersheds steelhead are most likely to spawn.

We use our model to predict steelhead redd density and abundance above barriers to passage within the four watersheds. We then estimate multiple metrics that can be used for prioritizing barriers for removal. Removal of manmade barriers to fish passage is suggested as a reasonable action during the first stages of recovery planning for listed salmonids, including winter steelhead in the Willamette River basin, because it has a high likelihood of success and a very low likelihood of negative impacts (Roni et al. 2002). However, removing or correcting passage barriers is expensive, limiting the rate at which these problems can be addressed. In the absence of detailed field data, identifying which barriers might have the greatest impact on fish abun-

dance, and hence should be removed first, is a difficult problem. Our broad-scale analyses use existing data to support making management decisions for listed salmonids.

Materials and methods

Study area

The Calapooia, North and South Santiam, and Mollala watersheds in the Willamette River basin drain the western slopes of the Cascade Range, Oregon (Fig. 1). Annual precipitation ranges from 1000 to 5500 mm and increases with elevation. Most precipitation falls from November through March and highest river flows usually occur in December and January. Private and federal forests dominate the higher elevations of all four watersheds; agriculture is the dominant land use in the lower elevations.

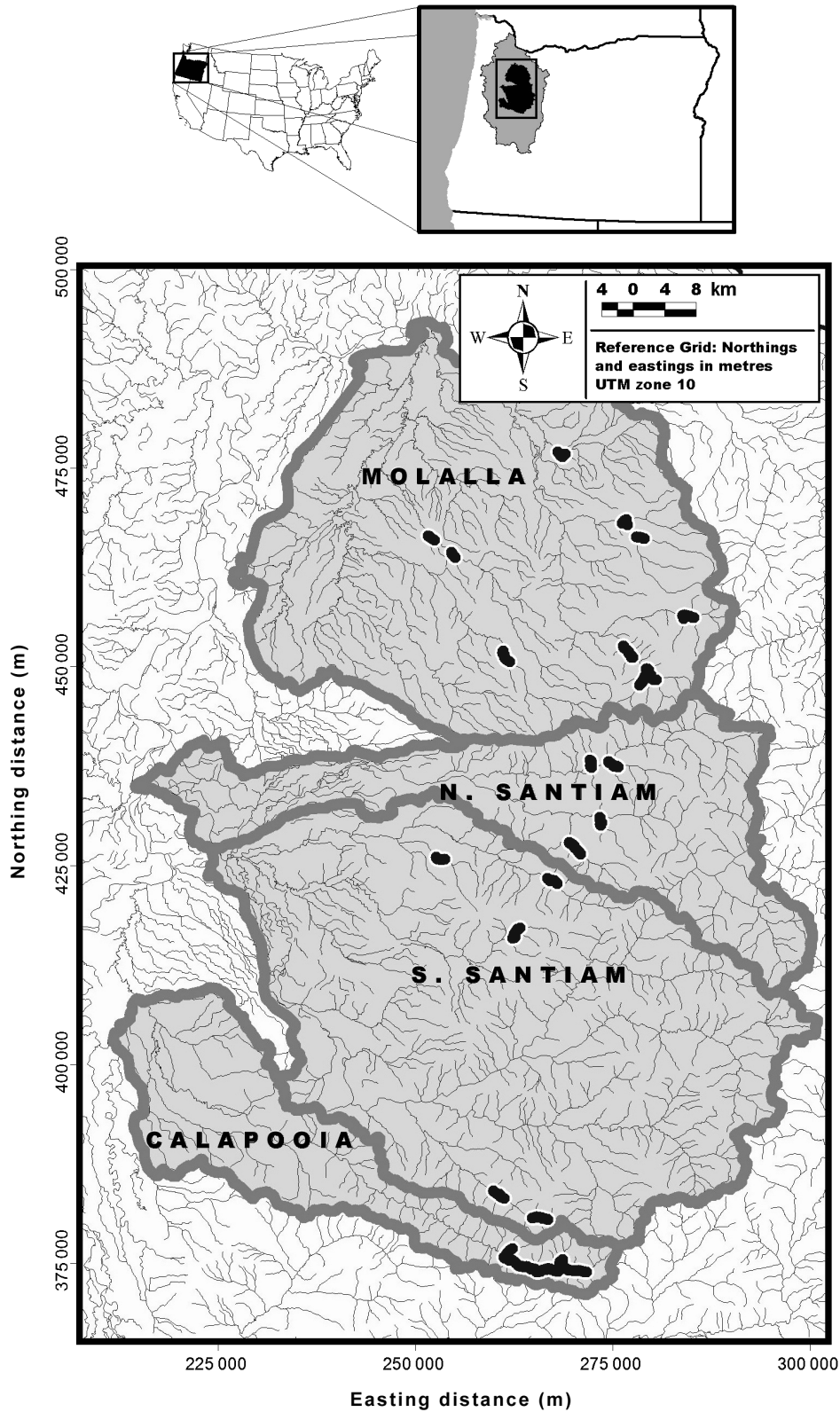
Steelhead data

Steelhead populations listed under the Endangered Species Act (ESA) in the four watersheds are winter steelhead that enter fresh water in March and April and spawn soon after arrival. Spawning occurs primarily in the lower gradient reaches of the watersheds. After emergence, juvenile steelhead generally spend 2 years rearing in fresh water. Between seasons, juveniles may stay in the main channel, move upstream into smaller tributaries, or migrate downstream and then into tributaries.

We used annual steelhead redd surveys conducted by the Oregon Department of Fish and Wildlife between 1979 and 1999 at 27 index reaches distributed throughout all four watersheds (Fig. 1). Index reaches were georeferenced to US Geological Survey 1:100 000 scale digital line graph hydrographic data layers. Redd counts were normalized to the length of stream surveyed (redds per kilometre). These data provide the best available record of steelhead redd distribution in the Willamette River basin; however, sites were not randomly selected for this type of analysis. Sites were chosen to monitor specific populations of interest and therefore summarize the best steelhead spawning areas in the four watersheds rather than all available habitats.

These data may include some naturally spawning hatchery winter steelhead; however, the impact of hatchery introductions of winter steelhead on index reach redd counts in the study watersheds is limited. There is no hatchery program on the Calapooia River and hatchery winter steelhead smolts were only released into the South Santiam River during a 7-year period in the 1980s. There have been significant hatchery introductions in the Molalla since the 1960s; however, hatchery fish in the Molalla are of Big Creek origin and spawn in January and February, too early to be detected in the index reach surveys conducted in April and May (Chilcote 1998). There is a hatchery on the North Santiam River where hatchery fish made up about 17% of the run by the late 1990s. There is no estimate of what fraction of naturally spawning fish in the North Santiam River might be of hatchery origin. The redd count data do not include information about juvenile steelhead distribution or survival of eggs and fry from these sites. For this analysis, we limit our interpretation to redd distribution and do not infer that sites with consistently high numbers of redds necessarily produce large numbers of juveniles or are adjacent to prime juvenile habitat.

Fig. 1. The four study watersheds, their location in the Willamette River basin, and the Willamette’s location in Oregon, USA. Black stream segments indicate Oregon Department of Fish and Wildlife index reaches used in this analysis.



Landscape data

Our choice of landscape variables to be tested in model development was based on published relationships between

site-specific habitat characteristics and steelhead distribution (Bustard and Narver 1975; Reiser and Bjornn 1979) (Table 1). We expect that substrate, water velocity, and depth

Table 1. Predictor variables used in model building, the categories used to create the predictor (if the name in the data layer is different from predictor name), whether the predictor was calculated as a proportion of the watershed draining to the index reach or as area-weighted mean (AWM) of the values within that watershed, whether the variable was entered as a continuous variable (C) or as an indicator (I) or both (although only one could remain in a model), and the data layer from which the predictor was derived (Appendix A).

Predictor	Categories/description	Calculated	Type	Data layer
Hillslope	Hillslope gradient < 6%	Proportion	C	Hillslope
Channel gradient	Range = 0.0–7.7%	AWM	C	Channel slope
Junctions	Range = 0.0–0.2 junctions·km ⁻²	AWM	C	Stream junctions
High hazard	High	Proportion	C	Debris flow hazard
Moderate hazard	Moderate	Proportion	C	
Min. temperature	Range = 2.16–5.07 °C	AWM	C	Air temperature
Max. temperature	Range = 10.98–15.68 °C	AWM	C	
Temperature range	Range = 8.61–11.55 °C	AWM	C	
Precipitation	Range = 1012–5560 mm	AWM	C	Precipitation
Alluvium		Proportion	C, I	Major lithology
Glacial drift		Proportion	C, I	
Landslide		Proportion	C, I	
Mafic intrusive		Proportion	C, I	
Mafic volcanic flow		Proportion	C, I	
Sandstone		Proportion	C, I	
Siltstone		Proportion	C, I	
Bedrock	Calc-alkaline volcanoclastic + mafic volcanic flow + mafic pyroclastic + felsic volcanic flow	Proportion	C	
Bare	Bare rock + sand + clay	Proportion	C	US Geological Survey national land cover for Oregon
Grassland	Grasslands + herbaceous	Proportion	C	
Open water	Open water	Proportion	C, I	
Shrub	Emergent herbaceous	Proportion	C	
Wetlands	Wetlands + woody wetlands	Proportion	C, I	Willamette River basin land use and land cover
Agriculture		Proportion	C, I	
Built		Proportion	C, I	
Old forest	FCC > 80 years	Proportion	C	
FCC total	All FCC classes combined	Proportion	C	
Young forest	FCC ≤ 40 years	Proportion	C	
Recent cut forest	FCC ≤ 20 years	Proportion	C	
Hardwood	Closed + semiclosed hardwood	Proportion	C	
Old hardwood	Forest closed hardwood	Proportion	C	
Young hardwood	Forest semiclosed hardwood	Proportion	C	
BLM	Bureau of Land Management	Proportion	C, I	Land ownership
ORCA	Oregon and California lands	Proportion	C	
USFS	US Forest Service	Proportion	I	
Private	Private or nongovernment	Proportion	C	
Road density	Road kilometres per unit area of catchment (length·km ⁻²)		C	Roads
River density	Stream kilometres per unit area of catchment (length·km ⁻²)		C	Streams
Catchment area	Total area of catchment for a given index reach		C	Catchments

Note: An indicator variable takes on a value of 1 if that feature is present in the watershed draining to the index reach or 0 if it is not present. FCC, forest cover class.

affect the distribution of steelhead spawners, as these characteristics influence spawning ability and the intragravel environment for successful incubation (Reiser and Bjornn 1979; Pauley et al. 1986). The landscape attributes that we included in our analyses have the potential to influence these finer scale habitat attributes that, in turn, influence steelhead redd density and distribution. We focused on characteristics associated with water quality (road density, land use), water

quantity, depth, and velocity (precipitation, hillslope, channel gradient) and on lithology and topography, which form the template for unit-scale habitat features (Benda et al. 1992; Beechie et al. 2001). Landscape variables were calculated from existing geospatial data layers (Table 1; Appendix A). These data layers included information about geology, climate, the land surface, forest cover, land ownership, and other human impacts such as road density and

dams. To calculate values for the landscape variables associated with each index reach, we delineated the watershed draining to that particular reach. We quantified landscape variables within the delineated watersheds using area-weighted mean for continuous variables and fraction of total area for categorical variables.

Three additional landscape variables were calculated: channel gradient (percent), number of tributary junctions, and drainage density (river kilometres per square metre). We included channel gradient because it drives the distribution of habitat units such as pools and riffles as well as water depth and velocity (Bjornn and Reiser 1991; Montgomery et al. 1999). Steelhead spawning is thought to be associated with a fairly narrow range of channel gradients. We included the number of tributary junctions and drainage density for two reasons: location of tributaries within a basin may explain fish community structure (Osborne and Wiley 1992) and tributary junctions may be areas of high biological productivity (Rice et al. 2001).

We inventoried all barriers likely to be impassible to steelhead within the watersheds using a combination of data sources: culvert locations and passage information from the Oregon Department of Fish and Wildlife Fish Passage Division (C. Corrarino, Fish Screening and Passage Program, Oregon Department of Fish and Wildlife, 2501 SW First Avenue, Portland, OR 97207, USA, unpublished data), western Oregon dams and natural barriers to fish (StreamNet 2001), Bonneville Power Administration dams and possible hydroelectric development sites (Pacific Northwest Hydropower Database and Analysis System Database, NWHS Database Management Group, Bonneville Power Administration, Portland, OR 97207, USA, unpublished data), and Interior Columbia Ecosystem Management Project (ICBEMP) dams with >10 acre feet storage capacity (1 acre foot = 1233.482 m³), originally from US Army Corps of Engineers (Quigley et al. 2001) as well as current anadromous fish distribution (StreamNet 2001), nonspatial databases, personal communications with state agencies, and published limits to fish passage by barrier height (Aaserude 1984). There is uncertainty associated with the barrier classifications because positional inaccuracy of some barriers prevented us from associating them with the stream network and because many barriers do not have complete passage information. Where passage status could not be determined, barriers were not included in our analysis.

We estimated the amount of available habitat above each barrier based on a 1 : 24 000 scale hydrographic stream network with geomorphically designated stream reaches generated from a drainage-enforced digital elevation model (DEM) (Miller 2003). Stream reaches were attributed with channel gradient, also calculated from the DEM. We calculated the total number of stream kilometres blocked by each barrier as the distance upstream from that barrier to a natural barrier. We eliminated streams with channel gradient >20% from our analysis, as these are rarely used by winter steelhead (Washington Department of Fish and Wildlife 2000). We limited redd density predictions to areas above barriers that have suitable spawning gradients and that are therefore most similar to the index reaches for which the models were built. We estimated available lengths of spawning habitat us-

ing two gradient windows. Stream segments with a channel gradient of 0.5–6% were identified as possible spawning segments. A subset of these stream segments, those with channel gradient ranging from 1% to 5%, were identified as likely spawning segments.

Model fitting and selection

Our purpose in building a model was to identify correlations between the distribution of steelhead redds and available landscape variables (Table 1) and to predict inaccessible reaches within the four watersheds that might also support large numbers of steelhead redds. Our model selection approach was designed to identify the best-fitting set of models for two specific and related purposes: (i) generating hypotheses about landscape factors influencing spawning suitability and (ii) predicting potential redd density in areas within these same watersheds for which redd count data do not exist. Our modeling approach had two distinct stages. In the first stage, we selected the model structure, including the covariance structure and random effects, and in the second, we selected the dependent predictor variables.

Model structure

We chose mixed models because they can accommodate correlated responses and heterogeneous variances. Since these spawner data were collected over time at the same sites, measurements within each site are serially autocorrelated. Using mixed linear models, we were able to model the autocorrelation and test the fit of various covariance structures (Littell et al. 1996). The Bayesian information criterion (BIC) was used to select the most appropriate covariance structure (Schwarz 1978). The BIC is essentially twice the log likelihood value plus a penalty for the number of parameters estimated; smaller values indicate a better fit. The BIC was calculated as follows:

$$\text{BIC} = -2l(\theta) + (p + q)\log(N)$$

where $l(\theta)$ is the maximized log likelihood function, p is the dimension of the model (i.e., rank(X)), q is the number of covariance parameters estimated (three for these models), and N is the sample size ($N = 384$ in our analyses).

We also investigated whether the slope and intercept should be modeled as random effects as in the random coefficients model or hierarchical linear models (Bryk and Raudenbush 1992) used in previous, similar studies (Pess et al. 2002; Feist et al. 2003). In this scenario, the slope, intercept, or both the slope and intercept for each year are allowed to vary randomly from an average slope and intercept. A random slope would indicate that the relationship between landscape characteristics and redd density varied by year. A random intercept would suggest that average redd density varied between years. An autoregressive covariance structure was assumed, as was independence between the slope and intercept. The appropriateness of possible scenarios was assessed by testing whether the variance of the slope and (or) intercept was significantly different from zero using both Wald and likelihood ratio tests (Casella and Berger 1990).

Variable selection

Variables in the final models were selected from all possible variables (Table 1) using a modified all subsets routine. A set of candidate models was selected using BIC (Schwarz 1978). The final models from within that set were selected based on metrics describing collinearity between predictors, the stability of the model coefficient estimates, and predictive accuracy. Models with high levels of collinearity between the landscape variables were eliminated using two criteria: pairwise correlation > 0.7 or condition index > 10 (Belsey et al. 1982). Models with values of Cook's $D > 1$ for at least one site were deemed unstable and eliminated from the analysis (Cook 1977).

A cross-validation procedure was used to assess model accuracy and precision. For each model under consideration, 10% of the observations were randomly selected as a validation set and were not used in coefficient estimation. Coefficients were estimated using the remaining 90% of the data and values were predicted for each observation in the validation set. The correlation (r) between the predicted and observed values was calculated, as was the root mean squared prediction error (RMSPE). The procedure was repeated 1000 times for each model, providing estimates of the mean correlation and RMSPE (measures of accuracy) and the variance of these statistics (measures of precision). Smaller variation was taken as an indication of a more stable predictive model.

Predicting steelhead redd density and prioritizing barrier removals

For each potential barrier in the study region, we determined the watershed area draining to that point from a 10-m DEM using the same technique employed above in determining landscape characteristics for watersheds draining to index reaches. For each barrier watershed, we calculated all landscape variables included in the final models to predict redd density. Steelhead redd density within the barrier watershed was predicted to be the average of the values from the set of best models, excluding those models for which one or more of the barrier watershed landscape values fell outside the range of values used in model building. We also calculated the relative number of new redds as the predicted redd density multiplied by the length of possible or likely spawning habitat. Ninety-five percent prediction intervals were calculated for all predictions using Proc Mixed in SAS.

Results

Redd distribution

The density of steelhead redds at the index reaches fluctuated over the 20-year study period; however, the ranking of the sites was less variable (Fig. 2). We found that steelhead redds were consistently found in greater abundance in some index reaches than in others and that those sites consistently supporting the largest fraction of redds were not clustered in one watershed but were distributed throughout all four watersheds (Fig. 2). These findings support the premise that landscape variables play a contributing role in determining locations of high densities of steelhead redds. Watersheds draining to individual index reaches ranged in size from 5 to 563 km².

Final models

Model structure

A comparison of the BICs for each of three covariance structures — autoregressive of order 1 (correlation decreases with measurements taken farther apart in time), compound symmetry (all correlations between years equal), and independence between years — indicated that the autoregressive model gave the best fit. This structure was used for all subsequent modeling. There was little evidence that the variance of the slope was different from zero but there was convincing evidence that the intercept should be considered a random coefficient ($p < 0.01$ for all one-variable models). The final model structure included an autoregressive structure with a lag of 1 year and a random intercept across years.

Variable selection

All 37 potential explanatory variables were fit independently. After the modified all-subsets procedure, there were 19 candidate models based on BIC alone. Four models were selected as the set of final models (Fig. 3; Table 2) based on correlation, RMSPE, and variance in their correlation estimates. The correlation between observed and predicted values for the four final models ranged from 0.618 to 0.642; the RMSPEs ranged from 0.808 to 0.827 (Fig. 3). The correlation between observed and predicted steelhead redd density was higher for the averaged predictions from all four models together (0.656).

Landscape variables included in the set of best models were the proportion of the watershed in alluvium, the proportion of the watershed with a hillslope $< 6\%$, the proportion of the watershed in ancient landslides, the proportion of the watershed in young (< 40 years) forest, the proportion of the watershed with shrub vegetation, the proportion of the watershed in agriculture, and the presence of mafic volcanic lithology. None of the models were able to predict years with redd counts of zero (Fig. 3).

Barrier prioritization

We identified 168 barriers within the study area as either unlikely to be passable or completely impassable (Fig. 4). Blocked kilometres of likely spawning habitat for any one barrier ranged from 0 to 67.2; blocked kilometres of possible spawning habitat ranged from 0 to 95.7. We estimate that the study area contains 874 inaccessible stream kilometres with channel gradients in the possible spawning range (0.5–6%); of these, there are 595 inaccessible stream kilometres with channel gradients in the likely spawning range (1–5%). Total stream kilometres blocked by anthropogenic barriers accounted for 32% of the stream length in the four watersheds. The amount of possible habitat blocked by anthropogenic barriers for any one watershed ranged from 30% (South Santiam) to 39% (North Santiam). Any errors resulting from uncertainty in barrier classification or positional inaccuracy have likely resulted in underestimates of inaccessible stream kilometres.

Predicted redd density upstream of barriers ranged from 2.3 to 22.4 redds·km⁻¹. These predicted values can be interpreted as the expected average redd density across many reaches for the average returning population size between 1979 and 1999. Because returns will vary in the future, these

Fig. 2. Distribution of steelhead redds by index reach from 1979 to 1999 in the North Santiam (NS), South Santiam (SS), Calapooia (C), and Molalla (M) watersheds within the Willamette River basin. The fraction of steelhead redds was calculated as the fraction of redd density observed in a particular year within a particular reach divided by the redd density observed over all reaches surveyed in that year. The box in the boxplot represents the limits of the middle 50% of the data; the line within the box identifies the median. Whiskers identify 1.5% times the interquartile range; broken lines outside the whiskers indicate individual observations that fell outside this range.

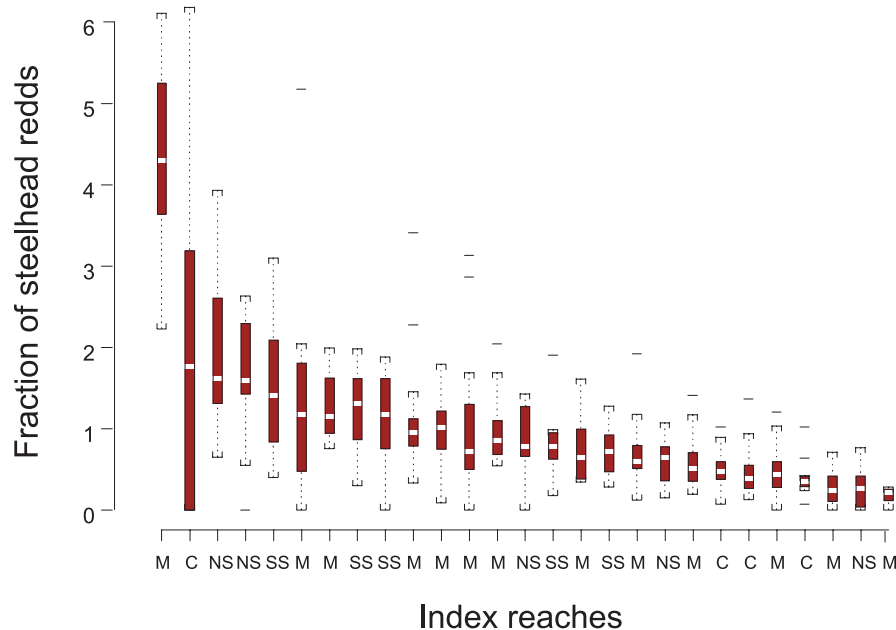
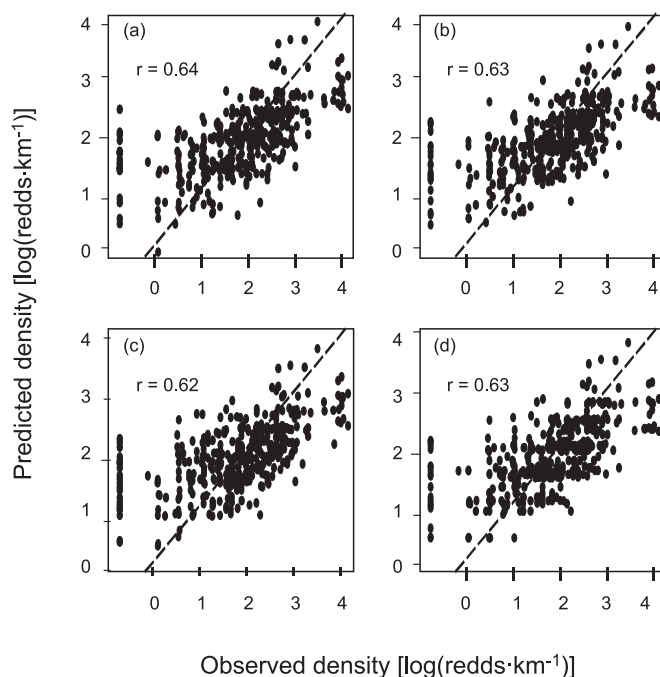


Fig. 3. Plots of predicted versus observed data in all reaches in the years 1979–1999 for the four models selected. The broken line is the 1:1 line. (a) $\log(\text{redds} \cdot \text{km}^{-1}) = 1.98 + 41.47 \times \text{alluvium} - 3.50 \times \text{hill-slope} - 1.08 \times \text{landslide}$; (b) $\log(\text{redds} \cdot \text{km}^{-1}) = 1.71 + 34.98 \times \text{alluvium} - 3.43 \times \text{hill-slope} + 12.41 \times \text{young forest}$; (c) $\log(\text{redds} \cdot \text{km}^{-1}) = 1.33 + 24.42 \times \text{alluvium} + 0.42 \times I(\text{mafic volcanic}) + 30.88 \times \text{shrub}$; (d) $\log(\text{redds} \cdot \text{km}^{-1}) = 1.59 + 37.79 \times \text{alluvium} + 0.47 \times I(\text{mafic volcanic}) - 8.38 \times \text{agriculture}$. $I(\cdot)$ is the indicator function: $I(\cdot) = 1$ if the feature is present, $I(\cdot) = 0$ otherwise.



predictions are best used in a relative sense to compare the potential of one site with that of another. Predicted number of redds if only the likely gradient range was used ranged from 0 to 1363 redds. If all possible gradient ranges were used, the maximum prediction increased to 1933 redds.

The modeled predictions of redd density provided new information for solving the problem of prioritizing barriers for removal. Predicted redd density identified five barriers blocking highly suitable habitat that would have been missed if one had simply used total stream length alone to identify candidate barrier removal projects (Table 3; Fig. 4). The modeled predictions also helped to distinguish between barriers that blocked large numbers of stream miles. There was over a threefold difference in predicted redd density between the two barriers that each blocked over 200 km of stream. The lower 95% confidence interval for redd density describes the lower bound of predicted redd density, the worst-case scenario. Using this metric, we can identify those barriers with the best worst-case scenario. Managers wishing to explicitly acknowledge the uncertainty in these modeled predictions might choose such a metric. This metric identified three barriers that would have been missed in a selection process that did not include uncertainty.

Fifty-seven of the 168 barriers were excluded from the barriers analysis because one or more landscape characteristics were out of the range observed for the index reaches used in model building. In all but one case, the proportion of alluvium was >0.0432 , the maximum observed for a watershed draining to an index reach used in model building. These barriers also had a larger proportion of agricultural land use than the maximum used for model building (0.1197). The excluded barriers were generally found in the

Table 2. Summary of final predictive models to predict $\log(\text{redds} \cdot \text{km}^{-1})$.

	Variable	Coef.	SE	Variance component	Estimate	Corr.	RMSPE
Model 1	Intercept	1.98	0.14			0.606	0.830
	Alluvium	41.47	7.77	Intercept	0.266		
	Hillslope	-3.50	1.08	Residual	0.704		
	Landslide	-1.08	0.35				
Model 2	Intercept	1.71	0.16			0.598	0.836
	Alluvium	34.98	7.38	Intercept	0.266		
	Hillslope	-3.43	1.11	Residual	0.721		
	Young forest	12.41	5.42				
Model 3	Intercept	1.33	0.18			0.585	0.850
	Alluvium	24.42	7.51	Intercept	0.238		
	<i>I</i> (mafic volcanic)	0.42	0.13	Residual	0.728		
	Shrub	30.88	11.93				
Model 4	Intercept	1.59	0.15			0.577	0.855
	Alluvium	37.79	7.48	Intercept	0.259		
	<i>I</i> (mafic volcanic)	0.47	0.13	Residual	0.711		
	Agriculture	-8.38	2.74				

Note: Coef., model coefficient; SE, standard error of the model coefficient; variance components describe the variance of the intercept and the residual variance of the model; Corr., correlation between observed and predicted redd density; RMSPE, root mean squared prediction error, describes the mean value from the cross-validation procedure.

lower parts of the drainage network and were distributed throughout all four watersheds (Fig. 4).

Discussion

Landscape factors affecting steelhead redd abundances in the Willamette basin

We found that the distribution of winter steelhead redds among sites in the Willamette River basin was fairly consistent over time. Our findings are in agreement with results from other basins and for other species (Pess et al. 2002; Feist et al. 2003) and, in combination, these results suggest that landscape features such as geology, vegetative cover, and climate should be good predictors of redd distribution in the future or in unsurveyed areas. The identification of multiple significant relationships between landscape features and steelhead redd distribution suggests that steelhead distribution is, at least in part, driven by factors operating at scales larger than those considered by traditional reach-scale models of fish habitat relationships. Consistent steelhead habitat relationships have been difficult to identify because of the flexible life history characteristics of steelhead and, perhaps, because of the emphasis on reach-scale habitat characteristics. The relationships identified here generate a series of testable hypotheses about the impacts of geology, landform, and land management on the distribution of steelhead redds.

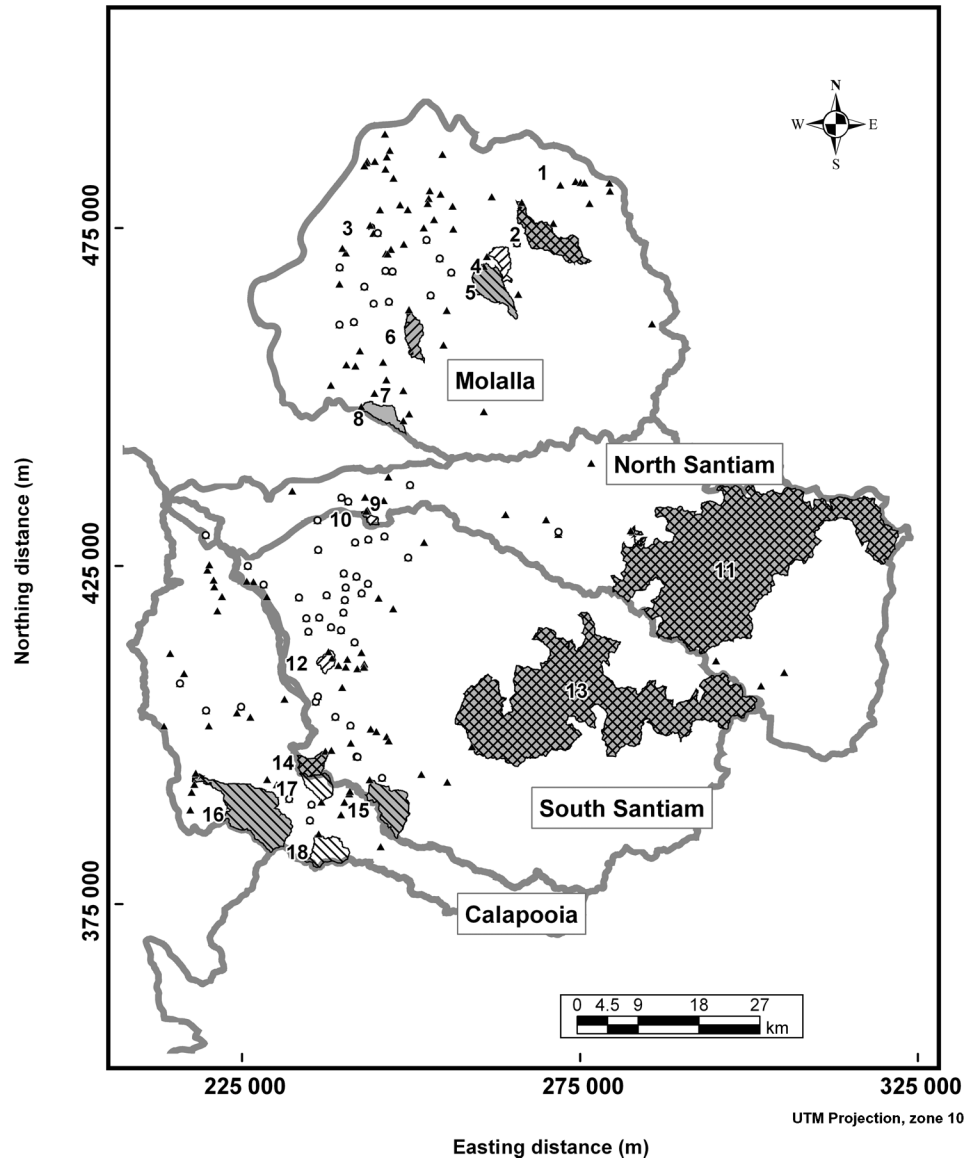
The most important variable in our models was the proportion of the watershed composed of alluvial deposits. In each of the four best models, the proportion of alluvium was a strong positive predictor of steelhead redd abundance. Areas with high amounts of alluvial deposits are more likely to have unconstrained channels with cobble substrate, which are preferred by steelhead (Bell 1973; Reiser and Bjornn 1979). It may also be that, in the four watersheds, areas with alluvium are simply correlated with some other feature preferred by spawning winter steelhead such as downstream ar-

eas or lower gradient areas. In either case, the correlation indicates that, within the study area, percent alluvium is a good predictor of areas that could support high numbers of spawning steelhead. The contributions of the indicator variable for mafic volcanic lithology and the proportion of landslide deposits reinforce the general hypothesis that the geology of an area plays a strong role in regulating the distribution of species. In addition, landform, the proportion of the watershed with hillslope <6%, was present in two of the best models.

We would expect that vegetation and land use might also be good predictors of winter steelhead redd abundance. Surprisingly, we found that the proportion of the watershed in shrub cover and in young forest were positive predictors of steelhead redd abundance. Shrublands were sprinkled in tiny patches across all four watersheds but were more likely in the upper watersheds. Shrubland includes areas "characterized by natural or semi-natural woody vegetation with aerial stems, generally less than 6 meters tall" (US Geological Survey 1999). A visual analysis indicates that these patches are associated with logging roads, so we conclude that much of the land designated as shrubland is clearcut. Young forests tended to be clumped around particular index reaches and were not clearly correlated with other potential predictors. A positive relationship between clearcuts or new forests and fish production has been reported elsewhere for juvenile fish (Murphy and Hall 1981; Bisson and Sedell 1984; Holtby 1988). In these previous studies, short-term, positive effects result from an increase in stream productivity following an increase in available sunlight. Steelhead may be more resistant than other species to some negative impacts of timber harvest management such as increases in winter discharge; as spring spawners, steelhead eggs are not exposed to the full force of winter high flows.

Potential impacts of hatchery programs were not considered in our analysis of landscape-scale habitat features; however, hatchery management clearly impacts the distribution

Fig. 4. All barriers identified within the study area. Barriers identified with solid triangles were used in the barrier prioritization analysis. Barriers identified with open circles were excluded because one or more landscape characteristics were out of the range observed for the index reaches used in model building. Watersheds are delineated for the nine barriers selected for further investigation as identified by each of three criteria: stream length (km) (diagonal lines sloping downward to the right), predicted redd density (redds·km⁻¹) (diagonal lines sloping upward to the right), and predicted number of redds in possible spawning areas (shaded areas). Numbers correspond to barrier identification in Table 3. Note: All barriers identified by both stream length and predicted redd density (cross-hatched) were also identified using predicted number of redds and therefore have a shaded background.



of wild spawning fish. There have been winter steelhead hatchery introductions in three of the four study watersheds and there has likely been some straying of hatchery fish into the Calapooia River (Chilcote 1998). As well, introduced summer steelhead may have a negative impact on wild winter steelhead through competition for feeding territories and spawning habitat (Chilcote 1998; Kostow et al. 2003). Detailed data on these introductions could likely explain some of the remaining variance in our models.

Advantages of the mixed-models approach

The mixed-models approach allowed us to model annual correlation explicitly, taking advantage of the information available in a 20-year time series of fish abundance data. Be-

cause mixed models allow for flexibility in the correlation matrix, we were able to calculate theoretically derived confidence intervals that can be tested or corrected using Monte Carlo simulations. Therefore, by using the mixed-models approach, we were able to develop a metric for prioritizing barrier removals that included uncertainty in model predictions. The mixed-models approach also allowed us to handle missing data. Although some sites were not surveyed every year, we were able to utilize the information that was available at those sites. While our data compared time series of redd abundances with static descriptions of landscape characteristics, the flexibility of our approach would enable analysis of a time series of landscape data if it were available. Using a time series of both fish and landscape data, our

Table 3. Prioritization information for the top nine barriers according to each of several criteria: total upstream length, predicted redd density, predicted number of redds considering either available lengths of possible or likely habitat, and the lower 95% confidence interval (CI) bound for the redd density prediction.

Barrier ID	Total upstream length (km)	Predicted redd density (redds·km ⁻¹)	Predicted redds (possible)	Predicted redds (likely)	Density lower 95% CI
1					5.07
2	67.05	8.52	354.22	286.10	
3		6.91			
4		7.37			5.41
5	40.48		74.14	55.41	
6		10.53	105.19	82.52	5.58
7					4.90
8			80.52	69.69	
9					4.98
10		7.22			5.32
11	265.88	22.36	1933.14	1362.65	12.56
12		6.89			
13	256.19	6.95	474.50	316.87	4.85
14	26.61	12.05	87.69		7.39
15	49.04		93.53	70.97	
16	85.57		176.26	118.08	
17	30.24				
18	30.74			45.07	

Note: Each row represents one barrier; barrier identification is used in Fig. 4. Empty cells indicate that the barrier was not in the top nine barriers according to that criterion. Predicted redd density values represent the average values from as many of the four best models as possible given that the habitat values for that barrier must fall within the range of values used to build the model. Barriers draining watersheds for which any variable was outside the range of variables used to build all four models were not included in this analysis.

modeling approach could answer questions about how fish populations respond to changes in landscape condition.

By testing a variety of model structures, we were able to learn something about the underlying relationship between landscape variables and redd distribution. The lack of evidence for a random slope despite the evidence for a random intercept implies that there is a consistent relationship between redd density and landscape characteristics that varies in magnitude from year to year as a function of population size. This model structure is consistent with our findings of relatively constant redd distribution patterns over time and our overarching hypothesis that landscape type and condition play strong roles in regulating the distribution of spawners, independent of population size.

Using model-based predictions of habitat suitability to prioritize barrier removal projects

The landscape model developed in this paper can be applied to inform decision-making for managing anadromous salmonids. Using remotely sensed data and a model of steelhead distribution built for this particular area, a series of empirically based prioritization schemes for barrier removal projects were developed. Each prioritization metric provides information that is useful for identifying high-priority barrier removal projects. The total length of stream above a barrier is clearly an important consideration and may provide information useful for other purposes such as maximizing the benefit of barrier removal for multiple species. Adding modeled redd density predictions allows a quantitative assessment of the relative value of the reopened habitat for winter steelhead. The total predicted number of redds in either

likely or possible areas combines information about useable stream length and the modeled predictions into a number that can be compared across projects. For example, one could ask whether the number of new redds behind a barrier to a short stretch of river with optimal spawning habitat might be higher than the number of predicted redds behind a barrier to a long stretch of predicted low-abundance habitat. By using different classifications for predicting likely and possible spawning areas, this approach can provide managers with a range of expected numbers of new redds and an indication of the uncertainty in the estimates.

A novel aspect of our analysis to inform decisions on barrier removals was the use of a prioritization metric, the lower bound of the 95% confidence interval, which explicitly incorporates uncertainty into the ranking scheme. Such a metric selects the best barrier removals given the lowest expected redd density in the stream sections above the barrier. The use of a metric like the lower bound of a confidence interval can also remove those projects that exceed a specified risk of negative effects. Other similar metrics such as the lower bound of the 64% confidence interval or the probability of observing redd densities > 0.5 fish·km⁻¹ could also be calculated and applied using our approach. In our analysis, the metric that included uncertainty selected high-priority projects that might have been missed if only stream length or predicted fish benefit were used. It also enabled a clear differentiation between the two highest-ranking projects according to either total stream length or predicted number of possible redds.

While no prioritization scheme can substitute for detailed field analysis, it can greatly reduce the time required for

such field surveys by identifying a set of projects most likely to be successful. Additional metrics such as cost, land ownership, viability of downstream populations, or recovery priorities would complement the prioritization schemes presented here. The best metric or set of metrics to use in a particular situation will depend on the exact goals of the project, the trade-offs that managers are interested in making, and the risks that they are willing to accept. Our prioritization scheme, as applied to the Willamette River basin, would be enhanced by data collection efforts in the lower parts of the drainage network where there are high proportions of both alluvium and agriculture. The current model is not suitable for these areas. A monitoring system for barrier removal programs (e.g., Pess et al. 2003) to benefit steelhead will enable refinements of potential steelhead abundance predictions.

In summary, there are two major findings from our research: landscape features can be used to describe and predict the distribution of winter steelhead redds and these models can be used immediately to improve decision-making for anadromous salmonids. The prioritization of restoration projects is a valuable application of broad-scale correlation models. Future improvements on this approach will need to consider models that incorporate simultaneous effects on multiple aquatic species. The validity of the approach can be tested after barrier removal projects are underway. In the short term, our empirical approach, based purely on remotely sensed landscape data and generally available data on redd abundance, provides a series of testable hypotheses to improve our understanding of the impacts of landscape form and condition on winter steelhead distribution and abundance as well as management tools to help prioritize potential restoration projects.

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Appendix A

Table A1. Geographic information system (GIS) data layers used in habitat analysis for the Willamette River basin, Oregon, USA.

Data layer	Map scale and grid-cell size	Description
Hillslope	1:24 k 30 m	Hillslope gradient generated from US Geological Survey (USGS) 30-m digital elevation model (DEM) using ARC/INFO. Calculated the slope of every 30-m grid cell in the DEM. Hillslope is the sum all of grid cells with slope < 6%
Channel slope	1:24 k 30 m	Calculated manually using USGS 1:24 k 30-m digital elevation models (DEM). Defined as rise (upstream elevation minus downstream elevation of index reach) over run (river kilometre length of index reach) multiplied by 100
Stream junctions	1:100 k na	Used ARC/INFO to calculate the density of stream junctions for each watershed from the USGS 1:100 k stream network data layer
Debris flow hazard	1:24 k 30 m	Data layer generated by Oregon Department of Forestry (2000). Naturally occurring debris flow hazard rating generated from slope steepness, geologic units, stream channel confinement, fan-shaped geomorphology, and historical information on debris flow occurrence (Robison et al. 1999)
Air temperature	Unknown 4000 m	Gridded annual maximum and minimum air temperatures from parameter-elevation regressions on independent slopes model (PRISM) (Daly et al. 1994)
Precipitation	Unknown 500 m	Total annual precipitation for 1989, considered a “normal” year from PRISM (Daly et al. 1994)
Major lithology	1:500 k na	USGS classification of geologic map units according to major lithology
USGS National land cover data for Oregon	1:250 k 30 m	USGS classification of land cover data from LANDSAT TM satellite imagery (level 2). Generated by USGS using Anderson et al. (1976) protocols
Willamette River basin land use and land cover	1:100 k 30 m	Land use and land cover ca. 1990 (USGS 1999) derived from LANDSAT TM 30-m pixel satellite data. Developed by the Institute for a Sustainable Environment at the University of Oregon for use by the Environmental Protection Agency (EPA) Pacific Northwest Ecosystem Research Consortium
Land ownership	1:100 k na	Land ownership for Willamette River basin compiled into digital format by the Oregon State Service Center for GIS in 1992 and 1993
Roads	1:24 k na	Polyline representation of the Willamette River basin road network ca. 1997. Source material includes Oregon Department of Transportation, US Forest Service, and the Bureau of Land Management. Developed by the Institute for a Sustainable Environment at the University of Oregon for use by the EPA Pacific Northwest Ecosystem Research Consortium
Streams	1:100 k na	Polyline representation of the Willamette River basin stream network generated by USGS
Catchments	1:24 k na	Polygon representation of total area upslope of the downstream end of any given index reach. Generated from a USGS 30-m DEM

Note: All data layers were generated by other entities (such as federal, state, and academic institutions), with the exception of hillslope, channel slope, and stream junctions, which we generated ourselves. The “k” after all of the map scales is an abbreviation for “kilo” or 1000; a map scale of 1:100 k is equal to 1:100 000. Grid-cell size is the size of each individual pixel or grid cell for raster-based data layers. Grid-cell size is presented below the map scale. na, not applicable.